

# A reciprocal transplant experiment within a climatic gradient in a semiarid shrub-steppe ecosystem: effects on bunchgrass growth and reproduction, soil carbon, and soil nitrogen

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## Abstract

We investigated the effect of climate change on *Poa secunda* Presl. and soils in a shrub-steppe ecosystem in south-eastern Washington. Intact soil cores containing *P. secunda* were reciprocally transplanted between two elevations. Plants and soils were examined, respectively, 4.5 and 5 years later. The lower elevation (310 m) site is warmer (28.5 °C air average monthly maximum) and drier (224 mm yr<sup>-1</sup>) than the upper elevation (844 m) site (23.5 °C air average monthly maximum, 272 mm yr<sup>-1</sup>). Observations were also made on undisturbed plants at both sites. There was no effect of climate change on plant density, shoot biomass, or carbon isotope discrimination in either transplanted plant population. The cooler, wetter environment significantly reduced percent cover and leaf length, while the warmer, drier environment had no effect. Warming and drying reduced percent shoot nitrogen, while the cooler, wetter environment had no effect. Culm density was zero for the lower elevation plants transplanted to the upper site and was 10.3 culms m<sup>-2</sup> at the lower site. There was no effect of warming and drying on the culm density of the upper elevation plants. Culm density of *in situ* lower elevation plants was greater than that of the *in situ* upper elevation plants. Warming and drying reduced total soil carbon 32% and total soil nitrogen 40%. The cooler, wetter environment had no effect on total soil C or N. Of the C and N that was lost over time, 64% of both came from the particulate organic matter fraction (POM, > 53 µm). There was no effect of warming and drying on the upper population of *P. secunda* while exposing the lower population to the cooler, wetter environment reduced reproductive effort and percent cover. With the warmer and drier conditions that may develop with climate change, total C and N of semiarid soils may decrease with the active fraction of soil C also rapidly decreasing, which may alter ecosystem diversity and function.

**Keywords:** climate change, culm density, *Poa secunda*, shoot biomass, soil

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## Introduction

Many climate-change scenarios predict a warmer and, perhaps, drier climate in the future (Skiles & Hanson, 1994; Shen & Harte, 2000). The suggestion that the future will be cooler and wetter is rarely considered in global climate change research although rapid cooling events have occurred during the Holocene (Mayle & Cwynar,

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1995). Long-term effects of climate change on temperate grasslands have been simulated with the conclusion that a 3 °C increase in weekly mean maximum and minimum temperatures would have little effect while a 50% precipitation change would be significant (Hunt *et al.*, 1991). Little information exists on the consequences of rapid climate change on ecological process (Shen & Harte, 2000). We examined the response of a perennial bunchgrass (*Poa secunda* Presl) and associated soils by transplanting intact soil/plant cores between high and low elevation sites.

Field-warming experiments have shown no effect on graminoid biomass (Harte & Shaw, 1995) or cover (Price & Waser, 2000) in subalpine meadows. Similarly, there was no effect of temperature or precipitation change on well-established perennial grasslands in England (Grime *et al.*, 2000). Reproductive phenology was advanced by soil warming in Colorado (Price & Waser, 1998) and in the Arctic (Arft *et al.*, 1999). Reproductive effort increased with increased temperature in the field-warming experiments of Price & Waser (1998) and Nylehn & Totland (1999). We tested the hypotheses that there will be no effect of a climate change on production characteristics and that climate change will affect reproductive effort in a perennial bunchgrass.

Carbon isotope discrimination in plants increases with increasing air pressure at lower elevations and with increasing temperature (Körner *et al.*, 1991). Michelsen *et al.* (1996) found that warming up to 4.9 °C at a constant elevation reduces  $\delta^{13}\text{C}$  in *Cassiope tetragona*. Carbon isotope discrimination can vary with precipitation (Schulze *et al.*, 1998), but does not vary with precipitation in semiarid winter precipitation areas in Patagonia (Schulze *et al.*, 1996). Leaf nitrogen increases with increasing elevation (Körner, 1989; Bowman *et al.*, 1999). A variety of changes in plant nitrogen have been observed in warming treatments in the Arctic (Michelsen *et al.*, 1996; Hobbie & Chapin, 1998). We tested the hypotheses that carbon isotope discrimination and plant nitrogen will be affected by climate change.

Soil carbon and nitrogen are reduced with increasing temperature in grasslands (Burke *et al.*, 1995a). Ojima *et al.* (1993), modelling the effects of climate change on grassland soil carbon, predict soil carbon will decrease with increased temperature. There is less soil carbon and nitrogen in a warm eastern Colorado prairie than in a cooler prairie in north-eastern Colorado (Burke *et al.*, 1995a). High elevation forest soils in the Cascades have higher carbon and nitrogen than do low elevation soils because of reduced mineralization rates with low temperatures (Hart & Perry, 1999). We tested the hypothesis that soil carbon and nitrogen will decrease in a warmer, drier climate and increase in a cooler, wetter climate.

The objective of this work was to examine the effects of climate change on intact soil-core microcosms of

*P. secunda*. Several plant and soil characteristics were measured 4.5 and 5 years after transplanting the cores. We also examined *in situ* *P. secunda* at both sites.

## Materials and methods

### Study area

Research was conducted on Rattlesnake Mountain in the Hanford National Monument of southeastern Washington. The area is semiarid, with most precipitation falling in the fall and winter (Thorp & Hinds, 1977). The lower elevation (310 m) site is warmer (28.5 °C air average monthly maximum) and drier (224 mm yr<sup>-1</sup>) than the upper elevation (844 m) site (23.5 °C air average monthly maximum, 272 mm yr<sup>-1</sup>), after Thorp & Hinds (1977). Both sites have a 2% slope. The aspect of the lower site is north (0°) and the upper site is northeast (60°). The soils of both sites, derived from the same basalt losses parent material, are a silt loam, forming for the last 3000–5000 years. Soils of both sites are a coarse-silty, mixed, mesic Xerollic Camborthids. Soil bulk density to a depth of 5 cm at the lower site is 0.96 g cm<sup>-3</sup> and 0.95 g cm<sup>-3</sup> at the upper site.

The plant community of the lower site is dominated by *Pseudoroegneria spicata* (Pursh) Á Löve and *Poa secunda* (Link *et al.*, 1990a). The upper site is dominated by *Artemisia tripartita* Rydb., *P. spicata*, and *Poa secunda*. *Poa secunda* Presl. is synonymous with *Poa sandbergii* (Vasey) or Sandberg's bluegrass (Hitchcock & Cronquist, 1976). It is a bunchgrass mostly less than 30 cm tall. The biologically active period for *P. secunda* and surface soils is from the fall through the spring when the soil is moist and temperatures are above freezing (Rickard, 1975). At a sandy site about 30-km south-east of the current study, phenological progression of *P. secunda* was delayed two weeks when irrigated in the spring (Link *et al.*, 1990b). The ability to measure low values of predawn xylem pressure potential was also delayed 10 days with irrigation. It flowers between April and late June across its range. It ranges from the Yukon and British Columbia, east of the Cascades, to California and east to Saskatchewan, Nebraska, and New Mexico (Hitchcock & Cronquist, 1976).

### Experimental design

Thirty-one cores with populations of *P. secunda* and soils were used in the experiment. An area of about 1000 m<sup>2</sup> at each site was chosen from which to extract cores and conduct the experiment. The experimental areas were chosen to be characteristic of native shrub-steppe. Areas with invasive species were avoided. Cores were randomly located within similar areas dominated by

*P. secunda* and *P. spicata*. Populations of *P. secunda* and soils were taken from interspaces between individuals of the larger bunchgrass, *P. spicata*.

Cores were encased in polyvinyl chloride (PVC) tubes 30 cm deep and 30.5 cm in diameter. The majority of *P. secunda* root mass is found in the top 10 cm of soil with little below 20 cm (Link *et al.*, 1990b), so the core depth is adequate to separate the experimental plants from external environments. The tubes remained in place during the experiment. Eight treatment cores were transplanted from the low to the high elevation site and vice versa. Control cores were extracted and placed in other holes at the same site with eight at the lower and seven at the upper site. Cores were dug and transferred on October 10 and 11, 1994.

Characteristics of the lower elevation, *P. secunda* population and soils experiencing the lower elevation climate (controls) are compared with those experiencing the upper elevation climate (cooler, wetter treatment). Similarly, characteristics of the upper elevation, *P. secunda* population and soils experiencing the upper elevation climate (controls) are compared with those experiencing the lower elevation climate (warmer, drier treatment). While we cannot separate effects of temperature and water on response in this experiment, we consider temperature to be a stronger factor than water because during most of the growing season the soils in the shallow root zones of *P. secunda* are equally wet at both sites. A large portion of precipitation drains below the roots of *P. secunda* becoming largely unavailable (Link *et al.*, 1990a). The higher precipitation at the upper site may initiate regrowth earlier in the fall than at the lower site and may extend activity later in the spring as was observed in Link *et al.* (1990b). Similarly, surface soils at the upper site may become active earlier in the fall and remain active later in the spring than at the lower site.

At each site, observations were made on *in situ* *P. secunda* populations in five replicate, 30-cm by 100-cm rectangular plots. This plot size fits into interspaces between surrounding individuals of *P. spicata*. Plots were located within 20 m of the cores. Comparisons are made between the two *in situ* populations.

### Measurements

**Plant density, culm density, percent cover, culm height, leaf length, shoot biomass** Plant measurements were taken on 17 dates between March 18 and May 10, 1999 making the length of the experiment for plants about 4.5 years. Plant and culm (jointed stem with leaves and flowers) density was determined in all cores and field plots. Each bunch was assumed an individual.

Percent cover was determined by measuring bunch dimensions. The greatest diameter ( $d_l$ ) and the greatest

diameter  $90^\circ$  to the greatest diameter ( $d_w$ ) were measured on all plants in the cores and in the field plots. An elliptical area of each bunch was computed as:

$$\text{Bunch area} = \pi * d_l * d_w / 4 \quad (1)$$

Bunch areas were summed to compute total percent cover. Percent cover was based on core area (730 cm<sup>2</sup>) and field plot area (3000 cm<sup>2</sup>).

In the cores, the height of the tallest culm in each of three bunches was measured repeatedly. Culms were initially measured on March 18 at the lower site and on April 14 at the upper site. Maximum culm heights were averaged for each core. The greatest leaf length was measured on all bunches in each core and field plot. Shoots (all above ground biomass) were harvested after seeds had formed and while the leaves were senescing. This occurred on April 18 at the lower site and on May 6 at the upper site. Shoot biomass samples were dried at 55 °C in a convection oven for 48 h and weighed.

**Stable isotopes, nitrogen content** Shoot samples were ground in a mortar and pestle for <sup>13</sup>C/<sup>12</sup>C and percent nitrogen determination. Percent nitrogen and the shoot carbon isotope ratio ( $\delta_s^{13}\text{C}$ ), relative to the PDB standard, were measured using a continuous flow isotope ratio mass spectrometer (IRMS) consisting of a Carla Erba 1108 Elemental Analyzer coupled through an open split interface with a Finnigan MAT Delta S IRMS. Calculation of shoot carbon isotope discrimination ( $\Delta$ ) after Farquhar *et al.* (1989) and Smedley *et al.* (1991) is

$$\Delta = \frac{\delta_a^{13}\text{C} - \delta_s^{13}\text{C}}{1 + \delta_s^{13}\text{C}} \quad (2)$$

where  $\delta_a^{13}\text{C}$  is the carbon isotope ratio of the atmosphere (−8.0‰) after Schuster *et al.* (1992).

**Soil carbon and nitrogen** Soil samples, in an air-dried condition, were collected from each site in 1994 and from each core in 1999. Soils were collected to a depth of 5-cm using a 2.54-cm diameter-coring tool. Soils were extracted from interspaces between *P. secunda* bunches. Lichens and moss were carefully removed without taking soils. Nitrogen fixing lichens were not observed in the cores although they are present in the area (Link *et al.*, 2000). Eight soil samples were taken in October 1994. Three samples were taken from each core on September 17 and 20, 1999, making the length of the experiment nearly 5 years. Samples were sieved through a 2-mm screen to remove roots and litter. Soils were fractionated into a < 53-μm mineral C fraction and a > 53-μm particulate organic matter (POM) fraction after shaking for 24 h in 0.5% Na-metaphosphate. Each fraction was analyzed for total C and total N by combustion analysis (Bolton *et al.*, 1993).

### Data analysis

Analyses were done using JMP version 2.0.2 software (Sall *et al.*, 1991). Student's *t*-test was used to compare means except for culm density. The Wilcoxon/Kruskal–Wallis nonparametric test was used to compare culm density values because of relatively large numbers of zero values. Error terms are one standard error of the mean. Statistical significance is set at the  $\alpha = 0.05$  level.

### Results

#### *Plant density, culm density, percent cover, culm height, leaf length, shoot biomass*

*In situ* plant density was the same at the two sites (Table 1). There was no effect of climate change on plant density in the cores (Table 2). No current year

culms were produced on lower elevation plants at the upper site, while significantly more culms were produced on lower elevation plants at the lower site (Table 2). There was no effect of moving the upper elevation plants to the lower site on culm density (Table 2). Current year culm density in the lower field plots was significantly greater than in the upper field plots (Table 1). Percent cover was reduced when plants were exposed to the cooler, wetter climate, while exposing plants to the warmer, drier climate had no effect (Table 2). *In situ* percent cover was the same at the two sites (Table 1).

Culms were first measured on day-of-year 77 (March 18) at the lower site in both upper and lower elevation plants, which is earlier than measurements on day 104 (April 14) in the upper elevation plants at the upper site (Fig. 1). No culms were observed in the lower elevation plants at the upper site (Fig. 1, Table 2). Culms of the lower elevation plants at the lower site increased in

**Table 1** Comparisons between *in situ* populations of *Poa secunda* from the lower and upper sites

Character	Field populations		<i>P</i>
	Lower population	Upper population	
Plant density (plants m <sup>-2</sup> )	87.7 ± 9.5	99.3 ± 5.0	0.27
Percent cover	24.6 ± 1.33	21.2 ± 2.83	0.30
Culm density (culms m <sup>-2</sup> )	26.7 ± 3.5	3.3 ± 1.8	0.0004
Greatest leaf length (cm)	3.78 ± 0.12	4.12 ± 0.27	0.28

Comparisons are made with Student's *t*-test (mean ± 1 SE, *n* = 5).

**Table 2** Comparisons between lower elevation *Poa secunda* plants plus soils when exposed to the cooler, wetter climate and between upper elevation plants plus soils when exposed to the warmer, drier climate

Character	Populations/soils in cores					
	Lower elevation plants/soil			Upper elevation plants/soil		
	at Lower site	at Upper site	<i>P</i>	at Lower site	at Upper site	<i>P</i>
Plant density (plants m <sup>-2</sup> )	54.8 ± 4.5, 8	54.8 ± 18.1, 8	1.00	70.2 ± 5.5, 8	70.5 ± 14.5, 7	0.99
Percent cover	25.8 ± 3.5, 8	11.7 ± 5.0, 8	0.038	37.9 ± 4.4, 8	30.3 ± 6.9, 7	0.35
Culm density (culms m <sup>-2</sup> )	10.3 ± 5.0, 8	0, 8	0.032	29.1 ± 12.0, 8	15.7 ± 13.5, 7	0.23
Greatest leaf length (cm)	5.10 ± 0.41, 8	3.21 ± 0.74, 8	0.043	5.64 ± 0.29, 8	4.62 ± 0.82, 7	0.23
Shoot biomass (g m <sup>-2</sup> )	3.30 ± 0.68, 8	2.12 ± 0.98, 8	0.34	7.23 ± 1.03, 8	7.31 ± 2.13, 7	0.97
Shoot carbon isotope discrimination (‰)	20.26 ± 0.13, 8	19.86 ± 0.37, 5	0.25	20.06 ± 0.24, 8	19.75 ± 0.13, 6	0.31
Shoot nitrogen (%)	1.21 ± 0.10, 8	1.60 ± 0.23, 5	0.10	1.23 ± 0.06, 8	1.82 ± 0.17, 6	0.004
Soil carbon (%)	0.87 ± 0.10, 7	0.88 ± 0.10, 8	0.94	1.36 ± 0.12, 8	1.99 ± 0.17, 7	0.010
Soil nitrogen (%)	0.06 ± 0.006, 8	0.06 ± 0.007, 8	0.66	0.09 ± 0.009, 7	0.15 ± 0.013, 7	0.002

Comparisons are made with Student's *t*-test (mean ± 1 SE, *n*) except for culm density, which is compared with the Wilcoxon/Kruskal–Wallis nonparametric test.

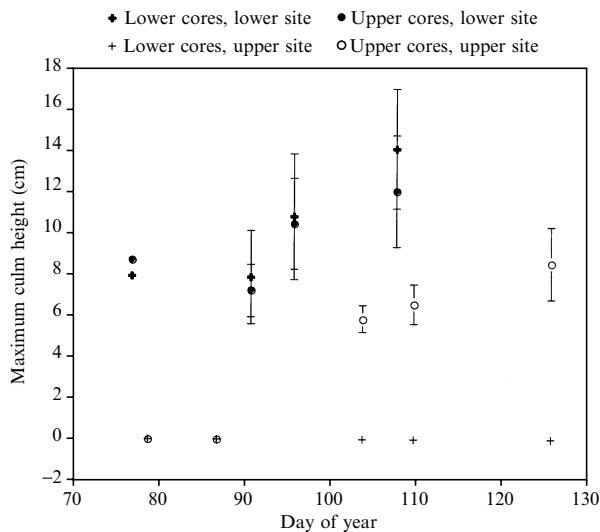


Fig. 1 Mean maximum culm height within cores. Error bars are one standard error of the mean.

length to about 14 cm by day 108 (April 18). Maximum leaf length was reduced when plants were exposed to the cooler, wetter climate, while exposing plants to the warmer, drier climate had no effect (Table 2). *In situ* maximum leaf length was the same at the two sites (Table 1). There was no effect of either climate change on shoot biomass (Table 2).

#### Stable isotopes, nitrogen content

There was no effect of either climate change treatment on shoot carbon isotope discrimination (Table 2). Percent shoot nitrogen was lower in plants that were exposed to the warmer, drier climate, while there was no effect on plants exposed to the cooler, wetter climate (Table 2).

#### Soil carbon and nitrogen

Percent soil carbon ( $0.88 \pm 0.007$  lower site;  $2.01 \pm 0.21$  upper site) and nitrogen ( $0.07 \pm 0.008$  lower site;  $0.14 \pm 0.02$  upper site) gathered in the field in 1994 were the same as in the control cores in 1999 (Table 2). Percent soil carbon and nitrogen did not change when soils were exposed to the cooler, wetter climate (Table 2). However, an average of 32% of the total soil C and 40% of the total soil N was lost when soils were exposed to the warmer, drier climate over 5 years. The decreases in soil C and N, for the upper cores were both highly significant (Table 2).

Fractionation of the total C pool showed that a significant loss of C occurred from both mineral-C and POM-C fractions (Fig. 2a). There was no significant change in C in either fraction when soils were exposed to the cooler, wetter climate. When soils were exposed to the warmer,

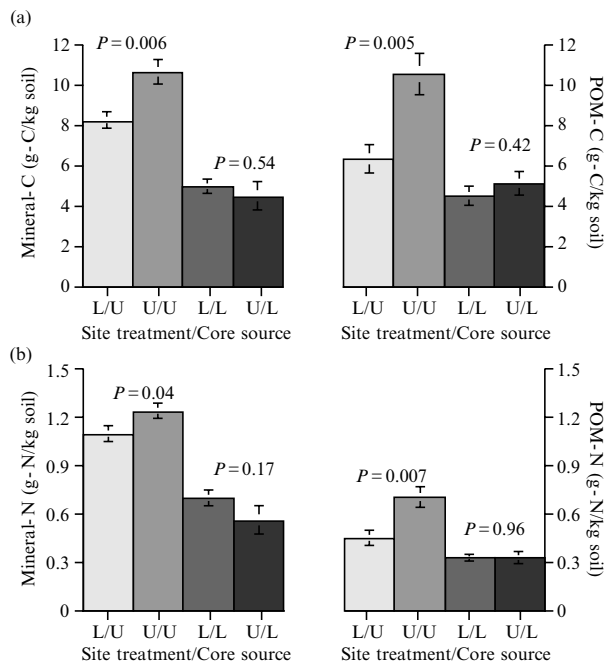


Fig. 2 The mineral ( $<53 \mu\text{m}$ ) and particulate organic matter (POM  $> 53 \mu\text{m}$ ) fractions of the total soil C (a) and total soil N (b) of the soil cores after 5 years. Significance of core treatments is noted with *P*-values. Error bars are one standard error of the mean (*n* as in Table 2).

drier climate, 64% of total C lost was from the POM-C fraction and 36% from the mineral-C fraction. Thus, the POM fraction lost approximately 80% more C than did the mineral fraction.

The fractionation of the total soil N, from the upper-transplanted cores, into POM-N and mineral-N showed trends similar to soil C. There was a significant loss of N from both soil fractions for these cores (Fig. 2b). The POM-N fraction accounted for 64% of the total N loss and the mineral-N for 36% of the loss. There was no significant change in soil N in either fraction when soils were exposed to the cooler, wetter climate (Fig. 2b).

#### Discussion

Our results depend on the conditions of the experimental system. The cores separate test plants from other species outside the cores, thus modifying root interactions. Our results may allow inference to conditions where *P. secunda* is the dominant species.

#### Plant density, culm density, percent cover, culm height, leaf length, shoot biomass

Our results support the hypothesis that the warmer, drier climate would have no effect on production

characteristics (plant density, cover, leaf length, shoot biomass), a result similar to studies in other ecosystems dominated by perennial plants. Shoot biomass was not related to increased temperature in the alpine perennial herb, *Saxifraga stellaris* (Sandvik & Totland, 2000). Similarly, warming had no effect on graminoid biomass (Harte & Shaw, 1995) or cover (Price & Waser, 2000) in a subalpine arid meadow, nor in perennial grasslands in England (Grime *et al.*, 2000). Perennial grasses are successful in nutrient-poor and stressful habitats such as the shrub-steppe by employing a conservative (nutrients are recycled within them) life history strategy that allows them to tolerate stressful conditions (Larcher, 1995). It is not likely that a 5 °C temperature increase is stressful for the upper elevation plants. *Poa secunda* is in warmer and drier environments at Hanford (Link *et al.*, 1990b) and elsewhere in the western United States (Hitchcock & Cronquist, 1976) where there is adequate winter precipitation. Increased temperatures and drier conditions may only have negative effects on plants near the warm and dry climatic edge of their geographical distribution.

Our results did not support the hypothesis that the cooler, wetter climate would have no effect on production characteristics after 4.5 years. We found reductions in percent cover, culm density, and leaf-length when plants were exposed to the cooler, wetter climate. Woodward (1979) found a smaller growth rate response to temperature in grass species from high altitude than in those from lower altitudes. *Poa* species from high altitudes can grow faster at low temperatures than *Poa* species from low elevations (Körner & Woodward, 1987). If these low elevation plants are more sensitive to a change in temperature, then the cooling at the upper site could account for production loss. In contrast, if the high elevation plants are less sensitive to temperature change, then this would explain the lack of growth effects in plants exposed to the warmer climate. Global warming may have smaller effects on plants adapted to cool environments based on our results and larger effects on plants adapted to warm environments (Woodward, 1979; Körner & Woodward, 1987). A similar conclusion can be drawn from Arft *et al.* (1999) who observed that warming in the cold High Arctic had a minor effect on growth compared with the stronger warming effect observed in warmer Low Arctic locations.

We found no support for the hypothesis that reproductive effort (culm density) would increase when plants were exposed to a warmer, drier climate. Others have noted increased reproductive effort with experimentally increased temperature in the field (Price & Waser, 1998; Arft *et al.*, 1999; Nylehn & Totland, 1999). The hypothesis that reproductive effort would be reduced in a cooler, wetter climate was supported by the data. This effect can be attributed to the small size of the plants (lower cover)

in the lower elevation cores at the upper site and the cooler, wetter environment. Reproductive effort is normally positively correlated with temperature and size (Larcher, 1995). Warmer conditions may explain why *in situ* plants at the lower site had much greater culm density than plants at the upper site though plant density and percent cover were the same. The small size of the lower elevation plants at the upper site and their exposure to cooler temperatures likely limits their ability to acquire sufficient carbon to support reproductive structures.

Culm initiation and growth was earlier in plants of both elevations at the lower site than at the upper site. Phenological advancement with warming has been observed in a variety of species in Colorado (Price & Waser, 1998) and in a number of grasses in the Arctic (Arft *et al.*, 1999). Phenological development in temperate grasses is strongly correlated with accumulated soil temperature (French & Sauer, 1974), so it is likely that phenology of *P. secunda* will advance with climate warming.

#### *Stable isotopes, nitrogen content*

Carbon isotope discrimination was not affected by climate change in this study. We expected carbon isotope discrimination to increase when plants were moved to lower sites with higher temperature, as discussed in Körner *et al.* (1991). Carbon isotope discrimination can change between 0.8 and 2.7‰, depending on species group, per km elevation change (Körner *et al.*, 1991). Our sites differed only 0.53 km in elevation so, we expected a significant difference of, between, 0.4 and 1.4‰. Michelsen *et al.*, 1996 found that warming up to 4.9 °C at a constant elevation significantly reduces  $\delta^{13}\text{C}$  in *Cassiope tetragona*. It is likely that the difference in elevation and temperature in our experiment was not sufficient to show an effect on carbon isotope discrimination in *P. secunda*. Carbon isotope discrimination in *P. secunda* may be relatively insensitive to changes in elevation and temperature compared with other species. An alternative explanation is that *P. secunda* may show genetic variation in carbon isotope discrimination, which could counter the effects of elevation and temperature. Variation in carbon isotope discrimination has been associated with variation in altitudinal seed source in a common garden experiment (Zhang *et al.*, 1993). Carbon isotope discrimination values in our experiment may not be directly comparable with values for plants experiencing a normal competitive environment. The roots of plants in the cores were most likely separated from those of the surrounding large bunchgrass, *P. spicata*. Carbon isotope discrimination can be increased in plants experiencing wet conditions (low water use efficiency) compared with those in drier conditions (Lajtha & Marshall, 1994; Schulze *et al.*, 1998).

We found support for the hypothesis, that shoot percent nitrogen would decrease when plants were exposed to warmer temperatures. Low elevation *Fraseria speciosa* plants have less nitrogen than high elevation plants (Bowman *et al.*, 1999). A possible reason for lower tissue nitrogen in high elevation plants exposed to the warmer climate may be lower soil organic matter. With lower organic matter content, microbial populations will be able to mineralize less organic nitrogen (Bolton *et al.*, 1990), thus plants will take up less nitrogen. We did not find support for the hypothesis, that shoot nitrogen would increase when plants were exposed to cooler conditions. Given that plant nitrogen increases with elevation (Körner, 1989), we had expected shoot nitrogen to become greater with exposure to cooler temperatures. A possible reason is that there also was no change in soil nitrogen.

#### *Soil carbon and nitrogen*

Our hypothesis that soil carbon would decrease when exposed to warmer, drier conditions was supported by the data. Thirty-two percent of the total soil organic carbon in the top 5-cm was lost when exposed to the warmer (5°C) drier climate after five years. This loss of carbon is likely because of increased soil respiration and carbon turnover rates with increased temperature (Schimel *et al.*, 1994) although it is possible that less carbon was allocated belowground accounting for a portion of soil carbon loss (Raich & Nadelhoffer, 1989). The observed reduction in soil organic carbon is greater than that predicted using the Century model with a 3°C-mean annual air temperature increase (Bottner *et al.*, 1995). Burke *et al.* (1995a) found 13% less soil organic carbon (top 5 cm) in 10–12°C warmer prairies of similar soil texture in eastern Colorado. The same conditions contribute to the 40% loss of total soil N in soils exposed to the warmer, drier climate. Some of the nitrogen loss in this ecosystem may be due to N<sub>2</sub>O loss from increased nitrification during periods of adequate moisture and higher temperatures (Mummey *et al.*, 1994, 1997). Some nitrogen may have leached from larger nitrate pools (Hart & Perry, 1999) below the shallow roots of *P. secunda*. It is possible there was less nitrogen input to the cores at the lower site that could account for some of the loss over the five-year period, but additions would be very small from biological and physical sources. We did not observe nitrogen fixing soil lichens in the cores and the soil algae are primarily green (Johansen *et al.*, 1993) limiting biological fixation. We did not observe an increase in soil nitrogen in cores taken to the upper site suggesting that physical deposition rates are similar and small at the two sites. The C and N losses due to soil warming in our study are far greater than those reported for tilled soil.

Tiessen & Stewart (1983) reported soil C losses of 65% after 60 years of tillage. Cambardella & Elliott (1992) reported reductions of 12–28% of total C and 11–19% of total N after 20 years in three agricultural management practices in grassland soils. Garten *et al.* (1999) indicate that a 4°C increase in mean annual air temperature could cause forest soils to lose 40–45% of their soil organic C inventories.

Soil C is mostly lost from the POM-C pool (Fig. 2). For the soils exposed to warmer, drier conditions, total C in the mineral C fraction decreased 22%, while the decrease in the POM fraction was 40%. In addition, the decrease in total N was 11% compared to 36% from the POM-N fraction. Thus, over time the C/N ratio of the mineral fraction will decrease. This differential loss is likely due to the low substrate quality of the C in the mineral-C pool (Smith, 1994). This C/N ratio difference is also evident from Fig. 2 where the g-C kg<sup>-1</sup> soil is similar for the mineral-C and POM-C fractions, however, the POM-N fraction constitutes only about one-third of the soil total N.

The loss of the POM fractions in these soils is likely to reduce the structural stability of microaggregates (Cambardella & Elliott, 1993). Soil organic matter facilitates the binding of microaggregates into macroaggregates (Jastrow *et al.*, 1996), which protects soil organic matter from decomposition (Beare *et al.*, 1994). Stabilized POM is more resistant to decomposition, thus the decrease in POM fractions and increase in aggregate turnover will further accelerate the loss of C and N from the system. The overall effect of the loss of POM fractions and reduction in mineral fractions is the loss of nutrients for plant growth, which will affect ecosystem function.

Our data do not support the hypothesis that soil carbon and nitrogen would increase with exposure to the cooler, wetter climate. There was no change in soil carbon or nitrogen after five years. Carbon capture rates and increases in total soil organic matter are very slow in semi-arid ecosystems (Burke *et al.*, 1995b). The plants had lower cover, no culm production, and shorter leaves suggesting that they were fixing less carbon, thus less carbon would enter the soil. Soil respiration may have matched a lowered rate of carbon input (Raich & Nadelhoffer, 1989) resulting in no accumulation of carbon. An examination of shoot and root carbon allocation and soil respiration rates would be useful to assess their contribution to soil carbon balance.

#### **Conclusions**

Our results suggest that the consequences of a cooler, wetter climate are severe for the lower elevation plants and likely to result in the loss of current populations. The

upper elevation plants are more likely to be successful in a warmer, drier climate.

Temperature is likely a strong factor explaining reduced production in our experiment. If *P. secunda* behaves as other *Poa* species (Woodward, 1979; Körner & Woodward, 1987), then populations adapted to warm temperatures will be less successful in a cooler climate. There was no reproductive effort in plants exposed to the cooler, wetter climate. The *P. secunda* populations may differ genetically. An investigation into the genetic basis for photosynthetic adaptations to altitude (Gurevitch, 1992) may show differences between *P. secunda* populations that can account for the effects of the cooler, wetter climate found in this study.

Soil C and N losses are a serious consequence of climate change. In this study, climate change resulted in a very rapid decrease in soil C and N compared to tillage, which can reduce SOM levels over long periods. The reduction in soil organic matter can affect the soil chemical, physical, and biological properties that contribute to ecosystem function and stability. The significant loss of C and N from the POM fraction of soil along with decreasing C/N ratios and increasing mineral SOM fractions can affect nutrient distribution patterns. Such changes may cause a shift in plant and microbial diversity leading to a functional change in the ecosystem.

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